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SENILITY AMONG GASTROPODS.

BY BURNETT SMITH.

INTRODUCTION.

The critical study of the development of Gastropod shell ornamentation has, until recent years, attracted the attention of few scientists in the United States. In Europe as early as 1889 Koken[1] made a careful study of Palæozoic Gastropods. This was followed in 1896 by the Countess von Linden's[2] study of the ornamentation and color patterns in *Voluta*, *Strombus* and *Conus*. In the United States, the first use of gastropod shell characters in the study of phylogeny occurs in the short notes of Heilprin[5] in 1888, dealing with the phylogeny of *Fulgur perversum* and *Strombus leidyi;* and of Leidy[4] and Wilcox on the ancestry of *Fulgur perversum*.

In 1900, A. W. Grabau presented a thesis at Harvard University dealing with the phylogeny of *Fusus* and allied forms. In June, 1902, the writer[5] applied the methods of the Countess von Linden to a study of the Fulgurs, and later in the same year A. W. Grabau[6] published a paper dealing with the general features of gastropod shell development. In 1903 Prof. Grabau[7] discussed the phylogenetic relations of the Fulgurs, and in the following year published an elaborate phylogenetic study of *Fusus*.[8]

In most of the above papers there is an attempt made to compare ontogeny with palæontogeny, dealing, therefore, with both recent and fossil forms. The individuals of species are studied from the earliest whorls to the latest, and the changes in shell features and ornamentation noted in the individual have been correlated with characters observed in the species of past geologic time. Where phylogenetic trees have been constructed they have been based on the principle that the individual in its development repeats, in its early stages, shell features which are found in the adult individuals of its ancestors. The authors have, for the most part, followed the principles applied and the laws formulated by Hyatt in his classic studies of the Cephalopoda.

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[1] Koken, E., "Ueber die Entwicklung der Gastropoden vom Cambrium bis zur Trias," *Jahrb. Mineral.*, 1889, Beilage, Band VI, pp. 305–484.

[2] Linden, Gräfen M. von, "Die Entwicklung der Skulptur und der Zeichnung bei den Gehäusschnecken des Meeres," *Zeit. Wiss. Zool.*, LXI, pp. 261–317.

[3] Heilprin, A., "The Geological Evidences of Evolution."

[4] Leidy, J., "Remarks on the Nature of Organic Species," *Tr. Wag. Inst. Phila.*, pp. 55–53, 1889.

[5] Smith, Burnett, "Phylogeny of the Species of Fulgur, with remarks on an abnormal specimen of Fulgur canaliculatum and sexual dimorphism in Fulgur carica," *Proc. Acad. Nat. Sci. Phila.*, June, 1902.

[6] Grabau, A. W., "Studies of Gastropoda," *Am. Nat.*, Vol. 36, p. 925.

[7] Grabau, A. W., "Studies of Gastropoda, II—Fulgur and Sycotypus," *Am. Nat.*, Vol. 37, pp. 515–539.

[8] Grabau, A. W., "Phylogeny of Fusus and Its Allies," *Smithsonian Miscellaneous Collections*, Part of Vol. XLIV (No. 1,417), Washington, 1904.

In any phylogenetic study of the gastropod shell, acceleration of the characters plays an important part. With the exception of *Fusus* and *Voluta,* most of the genera studied have been rather highly specialized and accelerated types like *Fulgur* and *Strombus.* In such forms many of the stages have been hurried back into the early whorls, slurred over or lost.

The writer feels that a detailed study of the shell features in some species of *Volutilithes,* as *Volutilithes petrosus* of the American Eocene, may add to our knowledge of the normal order in which such features are evolved. Several species of *Volutilithes* go through quite a number of stages of development in ornamentation, and there is little acceleration. Each stage, of course, does not necessarily represent an adult ancestor, for at present it is not known how much unequal acceleration of ancestral characters has come into play, yet nevertheless the writer feels that here we have a fairly normal and even succession of developmental features.

The occurrence of certain characteristics with considerable constancy in the later whorls of many individuals of *Volutilithes petrosus* has led the author to consider such features in other genera of gastropods. These features will be treated in the sections of this paper entitled *Senility* and *Senile Offshoots from Main Ancestral Stems.* The results of this later investigation are applied to *Fulgur carica,* in an endeavor to unravel its ancestry.

Normal Progressive Development.

In recording the characters which occur at different periods in the growth of any gastropod shell it is necessary to be exact; and this frequently results in the use of terms which appear arbitrary. The writer has, throughout this paper, endeavored as far as possible to apply the terms previously in use. Markings on the outside of the whorl which run parallel or nearly parallel to the suture are described as spiral; while those running across these spirals are described as transverse. The transverse markings which first appear are referred to as transverse ribs, or simply as ribs. When, in later stages, finer transverse markings appear between the ribs, they are described as riblets. Here the term is used principally for convenience, the actual difference between ribs and riblets being one of degree.

The angle which appears early on the rounded whorl is termed the shoulder angle. On the ribs, especially at the shoulder angle, may occur nodes or tubercles. These, in the early whorls, are mere rounded knobs; but in the later whorls they become larger, higher and sharper, and may therefore be referred to as spines. The writer considers that the difference between the small rounded tubercle of the early whorls and the large, sharp spine of the later whorl is one merely of degree. The word spine is therefore used, throughout this paper, simply in a descriptive sense, and implies no difference from the early tubercle, except that it is larger and sharper. Both are produced by the same fold of the mantle and every gradation between the two is observable.

As stated in the Introduction, *Volutilithes* has been chosen as an illustration on account of the normal and even course of its ontogeny. The stages are often very distinct, and frequently are all represented down to the senile condition in the later whorls. In addition, *Volutilithes petrosus* is of unusual interest on account of its individual variation and its division into more or less definite races, which exhibit different stages in the specialization of characters.

In the early stages of *Volutilithes petrosus* there is a varying number of smooth rounded whorls; but as a rule there are three or four. The first ornamental feature to appear on the rounded whorl is the transverse rib, which at first is simple (without tubercles) and usually decidedly curved. Soon the simple ribs are followed by uncurved ribs, bearing as a rule two tubercles, but sometimes more than two. One of these tubercles is situated at the suture, the other at the position of the shoulder angle. If more tubercles are present they are below the shoulder angle tubercle. Sometimes the suture tubercle and the shoulder angle tubercle are of the same size; but often they are of unequal size, and then it is usually the suture tubercle which is at first the larger. The suture tubercle, however, soon degenerates and becomes obsolete, while the shoulder angle tubercle increases in importance and by its increase in size and sharpness makes the spine of the later whorls.

Coincident with or shortly after the appearance of the tubercles on the ribs, a more or less well marked shoulder angle develops. As the shoulder angle tubercles become larger, sharper and more prominent the transverse ribs degenerate. This process begins first above the shoulder angle, where sometimes all trace of the rib has disappeared, when below the angle the rib is still well marked. As a rule, when the tubercles become very high and sharp (spines) the ribs practically disappear.

When fine spirals cover the early whorls below the shoulder angle, they are apt to disappear near the shoulder angle first in the later adult whorls. As the shell grows, these fine spirals are found in a more and more anterior position, until in old age only a few occur on the branchial siphon.

This briefly sums up the more important changes which are passed through in the development of most individuals of *Volutilithes petrosus*, and many other species of the genus. Many individuals and some races of *Volutilithes petrosus* pass through further stages of development; but these are all of a gerontic character, and may be now more fittingly discussed under the following section.

SENILITY.

In widely separated genera of gastropods the writer has observed that similar features are frequently found in the last whorl or in the last few whorls. These features are never followed, in any gastropod, by other and different ones, but are the last ornamental characters which the shell acquires. They are the marks of old age or senility. Many species and even genera and families never exhibit them, for in the Palæozoic they are rare and in the Mesozoic they are uncommon. In Tertiary and Recent time, however, few large families of gastropods are lacking in senile representatives. These representatives may be genera, species or individuals.

Individual Senility.—In many species, the vast majority of individuals die at the period of mature shell ornamentation. Senile characters are found only in an occasional specimen, which, as a rule, is either a very large old one or else a dwarfed or pathologic individual.[9] In individual senility, the senile features are seldom accelerated to any extent—that is, they are, as a rule, found in the last whorl, or in the latter part of the last whorl.

Specific Senility.—Often all the individuals of a species will show signs of senility in the last whorl, or in the last few whorls. This senile ornamentation of the species is more apt to be accelerated than the senile ornamentation of the individual; or, in other words, it occurs earlier in the growth of the shell.

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[9] A similar condition has been noted by Hyatt for the Cephalopoda: "Biological Relations of the Jurassic Ammonites," *Proc. Bost. Soc. Nat. Hist.*, Vol. XVII, 1874, p. 239.

Generic Senility.—Here all the species of a genus will exhibit signs of senility, and the generic senility is more accelerated than the specific.

Similarly, senility may extend to the genera of a family, and if, as is probably the case, the *Vermetidæ* are senile, we have the characters occurring early in the growth of shell, with the result that the forms comprising the family differ in appearance to a marked degree from the normal gastropod.

The marks of senility may be conveniently grouped under several heads. Two or three of them have been mentioned by Hyatt, Grabau and other authors, and these are merely noted in the present paper for the sake of completeness. The writer knows of no case in which all of the characters are found together. Frequently only one will indicate that the individual, species or genus has passed its prime, but more often two or more senile characters occur. As old age comes on the marks of senility appear, but not necessarily all at the same time. Usually one character will appear in the growth of the shell slightly ahead of another character. Sometimes one of the senile characters will be much accelerated and become prominent at a comparatively early stage, while the others will be found on the last whorl only.

The writer regards the following as marks of senility:

1. Passing of the shoulder tubercles or spines into a shoulder keel.
2. Swelling on the anterior siphon.
3. Protrusion of the mantle in the region of the anal siphon, producing a smoothing of the preceding whorl by a shelly overgrowth.
4. Encroachment of the anal siphon upward on the preceding whorl.
5. Stromboid form to the outer lip of the aperture.
6. Tendency toward loose coiling.
7. Irregularity of growth lines.
8. Thickening of the shell.
9. Tendency to form a smooth and rounded whorl.
10. Recurrent or discontinuous ornamentation.

1. *Passing of the shoulder tubercles or spines into a shoulder keel.*—This process is well shown in such forms as *Fulgur carica* and *Volutilithes petrosus,* where little acceleration has occurred. The change takes place by a shortening of the interval between spine formation, with the result that the spines are nearer each other. The growth lines, on which the spines are situated, are thus brought close together. The spines become lower in height, but longer in a spiral direction, until they fuse together into a continuous ridge, so that the final result of the process is a shoulder keel without definite spines.

In *Fulgur canaliculatum* acceleration has thrown the spines back into the early whorls, and they are mere tubercles. Their transformation into a shoulder keel is, however, essentially similar to the change in *F. carica.* The tubercles become longer in a spiral direction, but lower in height and soon merge into a shoulder keel.

2. *Swelling on the anterior siphon.*—In senile individuals and species the mantle, in the region of the anterior or branchial siphon, not infrequently bulges at a certain point. As the animal grows, this bulging of the mantle produces a swollen ridge in the shell. The long diameter of this swelling runs obliquely to the line of the shoulder angle, and in a more anterior direction. Numerous dissections of *Fulgur carica* have failed to show a cause for this mantle swelling.

The two above marks of senility—that is, the passing of the spines into a shoulder keel, and the swelling on the anterior siphon—are both well shown in old individuals of the *Fulgur carica* of our New Jersey coast. These two characters, together with a third (the tendency for the anal siphon to encroach upward on the preceding whorl), are the last ornamental features which occur on the oldest individuals. A well-marked sexual dimorphism occurs in this species. The full-grown males are considerably smaller than the full-grown females. The old males and old females show the senile characters above mentioned; and the difference in the size of the senile individuals of the different sexes furnishes a ready method of determining sex without reference to the soft parts. These observations were made on a large series of *Fulgur carica.*[10]

3. *Protrusion of the mantle in the region of the anal siphon, producing a smoothing of the preceding whorl by a shelly overgrowth.*—This is beautifully illustrated by several races of *Volutilithes petrosus.* In the later whorls the mantle in the region of the anal siphon protrudes and tends to wrap itself around the preceding whorl. In the early stages of the process we have little more than a smoothing of the preceding whorl. The mantle soon passes up over the spines of the preceding whorl, and the shelly deposit becomes thicker and thicker, completely obliterating ornamentation, and making it in many cases extremely difficult to count the whorls. Every stage of the process can be traced in individual development; while several races make a series from forms in which the mantle has been little protruded to forms in which it has covered in the preceding whorl, obliterating ornamental features. It does not necessarily follow that these races in question make a phylogenetic succession, but they unquestionably represent stages in the

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[10] *Proc. Acad. Nat. Sci. Phila.*, June, 1902.

development of certain features. The protrusion of the mantle onto the preceding whorl is often accompanied by an encroachment of the anal siphon upward onto the preceding whorl.

There is evidently a close relation between the swelling on the anterior siphon and the protrusion of the mantle on the preceding whorl in the region of the anal siphon; for as the latter feature becomes stronger the former declines. The races of *Volutilithes petrosus* above mentioned illustrate this fact perfectly. They range from forms with a well-marked swelling to others with no swelling; and in one race with an extreme mantle protrusion there is a depression in place of a swelling. As the swelling has been diminishing, there has been a corresponding increase in the amount of protrusion of the mantle on the preceding whorl in the region of the anal siphon.

4. *Encroachment of the anal siphon upward on the preceding whorl.*—This often accompanies the preceding mark of senility and is evidently produced by the same causes. It is well shown in *Volutilithes petrosus* and in *Fulgur carica,* also in *Strombus* and *Aporrhais,* where it is accompanied by the wing-like flaring of the outer lip of the aperture.

5. *Stromboid form to the outer lip of the aperture.*—This is a flaring, wing-like extension of the outer lip of the aperture and is found in *Strombus, Aporrhais* and a few other forms. In *Strombus* it is often accompanied by a thickening of the shell, by a bending of the branchial siphon upward or backward, by the encroachment of the anal siphon upward onto the preceding whorl, and by recurrent ornamentation (*Strombus leidyi*).

6. *Tendency toward loose coiling.*—In many gastropods the later whorls are not closely applied against the preceding whorls. In other words, the coiling becomes loose. *Ecphora, Rapana* and some species of *Murex* do not show signs of uncoiling until well along in life. In such forms as *Vermetus,* however, the process is further advanced, and all trace of the original spiral condition is lost at an early date; the shell becoming a mere irregular tube.

7. *Irregularity of growth lines.*—In many gastropods (*Volutilithes petrosus* is a good example) the final senile stages are characterized by a thickening and irregularity of the fine lines of growth. This character goes hand in hand with the thickening of the shell, the passing of the spines into a shoulder keel, recurrent ornamentation, and other senile features.

8. *Thickening of the shell.*—This is a character which occurs in the senile stages of many diverse groups of gastropods. It is usually accompanied by other senile features, and is probably more widely distributed than any other mark of senility.

9. *Tendency to form a smooth and rounded whorl.*—In many gastropods the later whorls tend to become rounded and more or less smooth, losing all ornamental features except growth lines and perhaps also fine spirals. In many individuals and varieties of *Fulgur pyrum* and related forms the shoulder keel stage is followed by a condition in which the whorl is rounded, the shoulder keel becoming fainter and fainter until it is not discernible. In many gastropods this rounded stage is accompanied by a thickening of the shell, but in others the shell actually becomes thinner. As the early whorls of most gastropods are rounded, it is possible that this mark of senility may be regarded as a recurrence of features of the same nature as the mark of senility next to be considered.

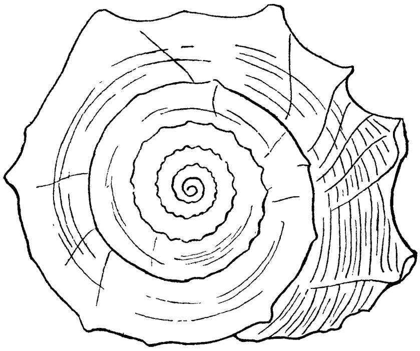


Fig. 1.—*Fulgur maximum* Con. Miocene. Cape Fear River, N. C. Diameter of shell across last whorl = 61 mm. Apical view exhibiting recurrent or discontinuous ornamentation.

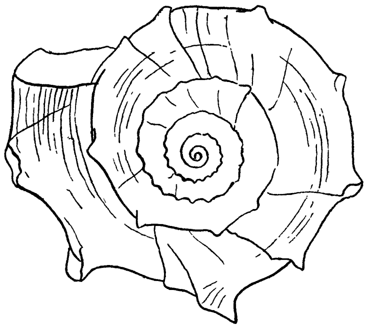


Fig. 2.—*Fulgur maximum* Con. Miocene. Cape Fear River, N. C. Diameter of shell across last whorl = 52 mm. Apical view exhibiting recurrent or discontinuous ornamentation.

10. *Recurrent or discontinuous ornamentation.*—This is a term which may be applied to the discontinuity produced by the repetition, at a later stage, of a style of ornamentation characterizing an earlier stage. Thus spines or tubercles which are found on the early whorls disappear for a few whorls, but are repeated as a secondary series in old age. The development of secondary spines is well shown in *Fulgur maximum.*

In most examples of this very variable species and its near relatives the shoulder angle tubercles are soon lost, and only reappear again in the later whorls, where they are spine-like and accompanied by features of extreme senility. Sometimes the arrangement of the shoulder angle spines may be considered as discontinuous, that is, where an occasional spine is met with on a rounded whorl. Here, as above, the condition is accompanied by other senile features.

Recurrent or discontinuous ornamentation is also met with in the sinistral *Fulgurs* of the Miocene, in not a few *Strombs,* and in some individuals of *Volutilithes dalli.* In the last mentioned, the breaks in a particular style of ornamentation may occur early in life, but the shell always shows senile characters in its last whorls.

SENILE OFFSHOOTS FROM MAIN ANCESTRAL STEMS.

In no group of gastropods are senile offshoots from main lines of descent so well marked as in the *Fulgurs.* The modern *Fulgur carica* of our New Jersey coast is a simple, little accelerated type which, however, shows well-defined senile characters in its last whorl.

In the Yorktown Miocene of North Carolina occur certain forms which were described by Conrad as *Fulgur striatum.* Some of these small forms are undoubtedly the young of *Fulgur maximum,* as can be seen in the early degeneration of the tubercles, but others whose tubercles increase in size can hardly be distinguished from the young of *Fulgur carica.* It is from these latter, or from very closely allied forms, that the modern New Jersey *Fulgur carica* is descended. The main line of the ancestry of *Fulgur carica* may be represented as follows:

MIOCENE.		PLIOCENE.	RECENT.
F. fusiformis or a nearly allied form.	Ancestral *F. carica;* probably included in Conrad's *F. striatum.*	*F. carica.*	N. J. *F. carica.*

This has been a slow and even evolution, marked by increase in size, stronger and continuous spine development, and finally in the old individuals of *Fulgur carica* by the appearance of the senile characters in the last whorl, which have already been referred to.

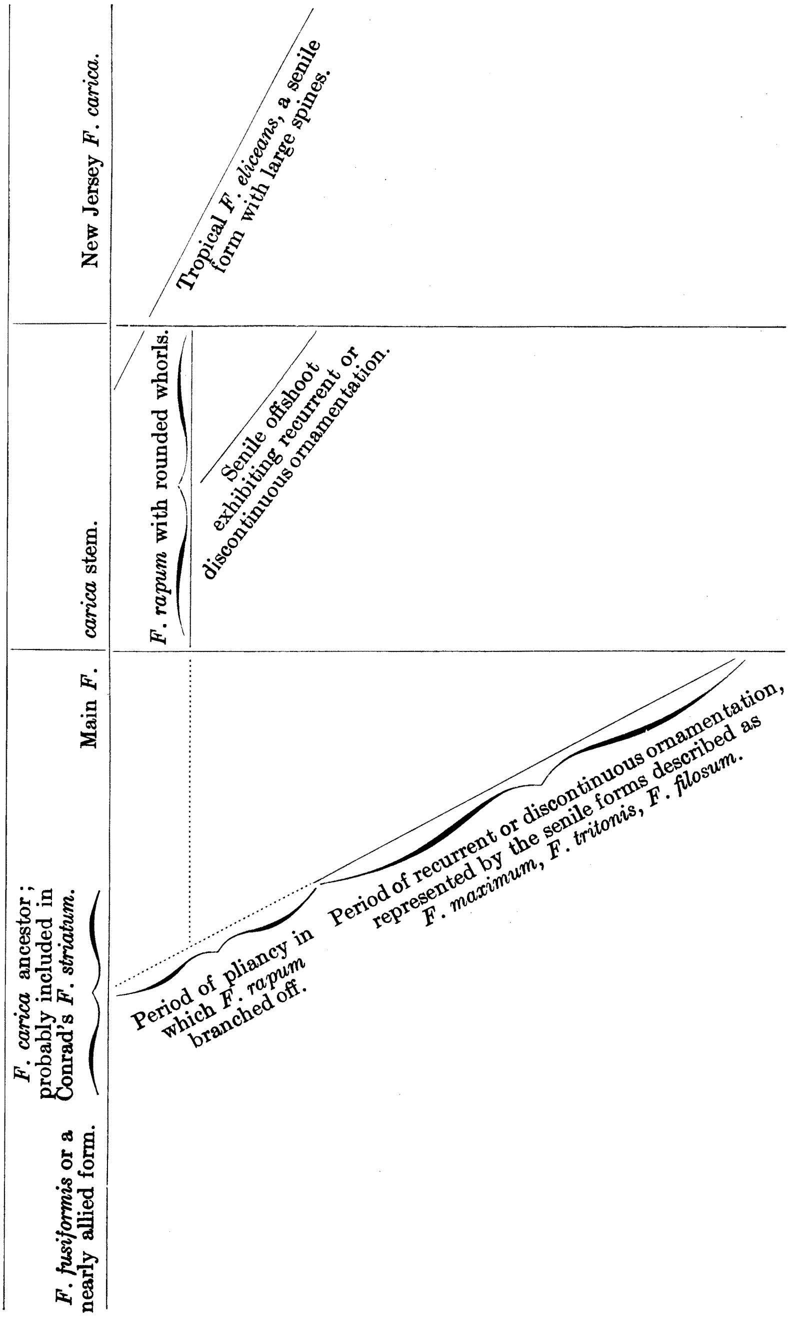
In the Yorktown Miocene the *Fulgur maximum* branch was evolved. As can be seen by examining the young *Fulgur maximum,* it owes its ancestry to the ancestral *Fulgur carica.* It differs from this form, however, in the early degeneration of the shoulder angle tubercles—a tendency which soon results in a rounded, lirate and relatively thin whorl. This spineless condition continues for some time, but in the later whorls secondary spines appear. This recurrent ornamentation is accompanied by shell thickening, encroachment upward of the anal siphon on the preceding whorl, and the swelling on the anterior siphon —all senile features. This is the method by which most of the individuals recognized as *Fulgur maximum* have been evolved. Sometimes, however, recurrent ornamentation is only slightly marked, the spines occurring at long intervals on the rounded whorls.

The whole assemblage shows every indication of being a senile offshoot. Every large individual shows senile characters. The main *Fulgur maximum* branch (including the forms described as *F. maximum, F. tritonis, F. filosum*) becomes extinct at the end of the Miocene.

Shortly after the divergence of the *Fulgur maximum* branch from the main *Fulgur carica* stem, a series of forms with rounded whorls diverged from the maximum stock. Their young are much like the young of *Fulgur maximum,* but the tubercles degenerate at a more early period. This short tubercled stage is followed by thin, rounded, spineless whorls in the vast majority of individuals, resulting in the form known as *Fulgur rapum.* A few senile individuals of *Fulgur rapum* exhibit a thickening of the last whorl, and recurrent or discontinuous ornamentation, in the shape of secondary spines. *Fulgur rapum* becomes extinct with the end of the Pliocene.

In Pliocene or Recent times a branch has been evolved from the *Fulgur carica* main stem which has resulted in such forms as *Fulgur eliceans.* These are senile and exhibit an acceleration of characters accompanied by very high spines. These spines are not as numerous as in *Fulgur carica.* They sometimes tend to pass into a shoulder keel, though less often than in *Fulgur carica.* In other respects, however, these forms show extreme senility—the swelling on the anterior siphon is very large, the shell is very heavy and the anal siphon encroaches upward.

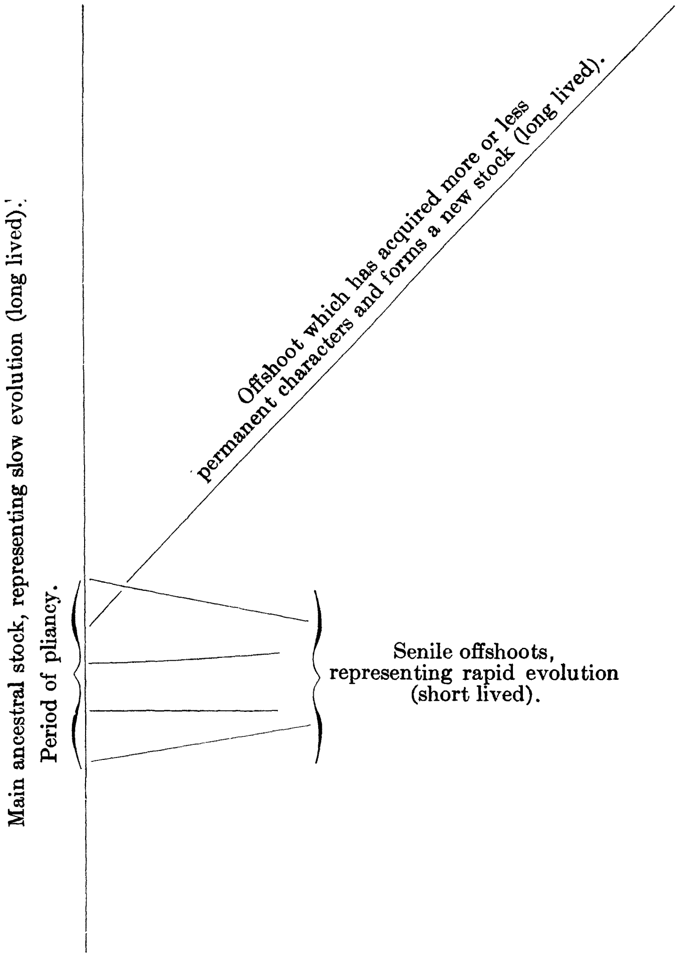
The phylogeny of *Fulgur carica* and allied forms may be represented as follows:


RECENT.
PLIOCENE.
MIOCENE.
New Jersey *F. carica.*
Main *F. carica* stem.
F. carica ancestor; probably included in Conrad's *F. striatum.*
F. fusiformis or a nearly allied form.
Tropical *F. eliceans*, a senile form with large spines.
F. rapum with rounded whorls.
Senile offshoot exhibiting recurrent or discontinuous ornamentation.
Period of pliancy in which *F. rapum* branched off.
Period of recurrent or discontinuous ornamentation, represented by the senile forms described as *F. maximum*, *F. tritonis*, *F. filosum*.

From the above study the writer is led to believe that there are two modes in which evolutional features may develop. First, they may develop slowly and evenly in the growth of the individual (ontogeny), and in the evolution of the race in geologic time (palæontogeny). Such forms are stable and persist for long periods of time. Second, the same evolutional features may develop in the same order, but more rapidly; one feature following another in quick succession in the ontogeny and palæontogeny. Such forms are apt to be short lived, soon becoming senile and dying out. Where the rate of development of evolutional features is rapid, we find that some features are slurred over; while other features may be more exaggerated than the corresponding features in the forms whose rate of development of characters is slow. Of course acceleration, or the throwing back of characters into the ontogeny, is a natural result of an increased evolutional rate.

Further, we cannot escape the conclusion that there are times in the evolution of a group of organisms (palæontogeny) which might be termed periods of pliancy. In these the simple, generalized members of the main ancestral stem can be easily moulded. At such periods of pliancy we may expect to find, first, forms which follow out the succession of developmental features, as in the main stock, but at a more rapid rate, becoming senile and extinct; and second, forms which acquire characters of a more or less permanent nature, and which do not go through the same succession of developmental features which is found in the main ancestral stock. These latter forms make new stocks, or, in other words, they go to form new species, genera, etc.

Therefore, at every period of pliancy in a stock we have, on the one hand, new species and, on the other, senile offshoots. In the forms above considered, that is, the *Fulgurs*, the numerous senile offshoots far outnumber the few but persistent stable forms. The following diagram may be used:


Main ancestral stock, representing slow evolution (long lived).
Period of pliancy.
Offshoot which has acquired more or less permanent characters and forms a new stock (long lived).
Senile offshoots, representing rapid evolution (short lived).

Adventitious Senility.

An acceleration of shell characters, produced by accident or by pathologic conditions, occurs in species of widely separated groups of gastropods. Hyatt[11] observed that "a wound and its results, whatever they may be, ... is primarily a severe shock to the system which lays additional burdens upon the powers of growth, and is usually followed, if severe, by retrogressive metamorphoses, or premature old age."

Individuals of *Volutilithes petrosus* whose shells in the later whorls have been subjected to breakage, often exhibit a sudden and sharp development of senile features. The shell gets heavy, the growth lines become irregular, and the spines tend to pass into a shoulder keel.

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[11] "The Genesis of the Tertiary Species of Planorbis at Steinheim," p. 15, *Anniversary Memoirs of the Boston Society of Natural History,* 1880.

An individual of *Ecphora quadricostata*, collected by the writer from the Maryland Miocene, exhibits acceleration produced by accident very clearly. The accident occurred to the shell during the development of the third whorl. From this point on the rate of the development of later shell features increases, and is much more rapid than in normal individuals. The individual in question never became mature, only attaining five whorls. A normal specimen with this number of whorls has practically no indication of loose coiling in the region of the columella, and the spiral folds are simple. The abnormal individual in question shows plainly a loose coiling in the columella region, and the spiral folds approximate those of more mature individuals. Loose coiling is, as a rule, not marked in normal individuals of this species until the seventh or eighth whorl.

A specimen of *Fulgur canaliculatum* collected at Longport, New Jersey, exhibits well the acceleration of characters produced by breakage in the shell.[12] In the canaliculate *Fulgurs* the transversely ribbed condition occurs very early, and is followed by a few angular whorls, bearing tubercles on the shoulder angle. These tubercles soon pass into a shoulder keel, and this in turn disappears, and leaves the whorl rounded, in the more accelerated forms, such as *Fulgur pyrum.*

Fulgur canaliculatum, however, never entirely loses the shoulder keel, which marks its last stage of development. In the specimen under consideration the accident occurred when the shell was young, on an angular whorl having the tubercles so characteristic of the early stages of *Fulgur canaliculatum.* After the break the shoulder angle is not reproduced, but the whorls continue to the aperture of a shape much as in *Fulgur pyrum.* Just after the break there is, apparently, an attempt to reproduce the tubercles on the rounded surface of the whorl. This attempt was, however, unsuccessful, and the whorl continued smooth. An examination of the soft parts showed the specimen to be identical with normal male individuals of the species, except that the shoulder angle is not present on the mantle. No peculiarity in the mantle edge or other soft parts could be detected which would account for the change in shell ornamentation.

The acceleration in this case has caused the dropping out of that marked character of the later whorls of the species, namely, the untubercled shoulder keel. On the other hand, it has introduced a senile character which occurs normally in a near relative (if not an actual descendant) of *Fulgur canaliculatum*, namely, *Fulgur pyrum*.[13]

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[12] Smith, Burnett, *Proc. Acad. Nat. Sci. Phila.*, June, 1902.

SUMMARY.

In most Mesozoic and Cenozoic gastropods, changes in ornamentation occur in going from the earlier to the later whorls. A normal succession of developmental changes may be observed, which varies little in widely separated groups; but most families show certain peculiarities in the succession which distinguish them from other families. Infancy, youth and maturity are represented by their peculiar styles of ornamentation in the ontogeny of an individual; but these stages, with their characteristic styles of sculpture, cannot always be correlated with the adults of a previous geologic time. This latter discrepancy may be due, in part, to the imperfection of the geologic record; but the writer inclines to the belief that the unequal acceleration of characters plays an important part, and that features which occurred at the same time in an ancestor are apt to be widely separated in the ontogeny of a descendant.[14]

In the last whorl, or in the last few whorls, of many gastropods of different groups we find the characters of senility. These characters or marks of senility do not necessarily appear together in the ontogeny at exactly the same time. Some occur far in advance of others; that is to say, there is frequently an unequal acceleration of the senile characters.

These senile features, several of which are, as a rule, found together, are the last characters which occur on the shell, for their appearance is the forerunner of the death of the individual. As might be expected, senile species or genera of fossil gastropods never transmit descendants to later geologic formations, but represent the end members of short branches on the phylogenetic tree.

The writer believes from his researches that the forces of evolution sometimes work rapidly and sometimes work slowly, and that the forms in which the evolutional rate is rapid are bizarre, senile offshoots. On the other hand, forms which have a long time range go through a slow evolution, though the developmental features and even the order of succession may be the same as in forms whose evolutional rate is a fast one.

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[13] There is good reason for believing that *F. pyrum* and its numerous varieties are descended from a Miocene form which is either identical with or closely allied to *F. canaliculatum*. See Smith, Burnett, *Proc. Acad. Nat. Sci. Phila.*, June, 1902, and Grabau, A. W., *Am. Nat.*, August, 1903, p. 521, and table, p. 539.

[14] Smith, James Perrin, "The Development and Phylogeny of Placenticeras," *Proc. California Academy of Sciences*, Third Series, Vol. I, No. 7, p. 185.

Lastly, an acceleration of characters may result from some accident which occurs to an individual; and in this case we may find a sudden appearance of senile characters, which may occur in the normal ontogeny of the species, at a later period, or they may be extra-specific; that is to say, never occurring in the ontogeny of the species, but found in some senile offshoot from the same stock.

The writer wishes to express his indebtedness to Prof. Amos P. Brown of the University of Pennsylvania, to Prof. Henry A. Pilsbry, Mr. Edward G. Vanatta and Mr. Witmer Stone of the Academy of Natural Sciences of Philadelphia, and to Mr. C. W. Johnson of the Boston Society of Natural History, for many courtesies and kindly suggestions and to Miss Helen Winchester for the care exercised in making the drawings.

EXPLANATION OF PLATES XXX AND XXXI.

PLATE XXX, fig. 1.—*Volutilithes petrosus* Con. Eocene. Mt. Lebanon, La. Length = 16 mm. Young individual, showing the change from simple curved ribs to straight tubercled ribs. In the last whorl the ribs are well marked below the shoulder angle, but very faint above it.

Fig. 2.—Apex of the above specimen. Length = 2 mm. Shows the change from simple curved ribs to straight ribs with suture and shoulder angle tubercles.

Fig. 3.—*Volutilithes petrosus* Con. Eocene. Jackson, Miss. Diameter of shell at last whorl measured on the largest spine = 24 mm. Apical view of old individual with long spines. Here the tendency for the spines to pass into a shoulder keel is only slightly marked, but they decrease in size rapidly toward the aperture. The last whorl is slightly smoothed by the protrusion of the mantle in the region of the anal siphon.

Fig. 4.—*Volutilithes petrosus* Con. Eocene. Bell's Landing, Ala. Diameter of shell at last whorl = 33 mm. Apical view of old individual exhibiting extreme senile characters, such as the passage of the shoulder angle spines into a shoulder keel, encroachment of the anal siphon upward, and the shelly overgrowth produced by the protrusion of the mantle in the region of the anal siphon.

Fig. 5.—A different view of the above individual. Length = 56 mm. Here the senile characters mentioned under Fig. 4 show up still more plainly, especially the passage of the shoulder angle spines into a shoulder keel.

Fig. 6.—*Ecphora quadricostata* Say. Miocene. St. Mary's River, Md. Length = 24 mm. Normal young individual.

Fig. 7.—*Ecphora quadricostata* Say. Miocene. St. Mary's River, Md. Length = 23 mm. Example of adventitious senility. Young individual which has been injured early in life and senile characters appear early. Tendency toward loose coiling is well marked.

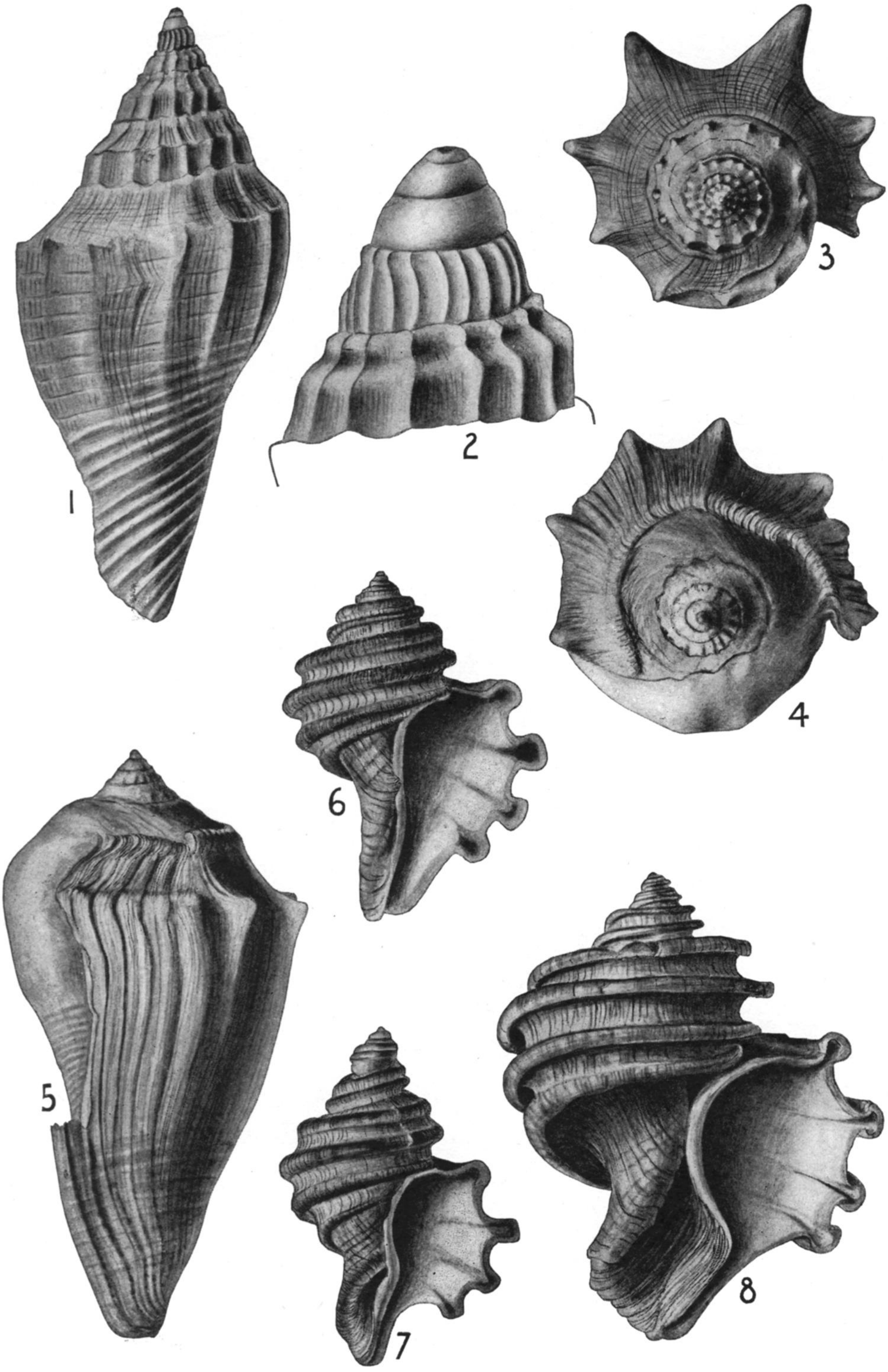
Fig. 8.—*Ecphora quadricostata* Say. Miocene. St. Mary's River, Md. Length = 76 mm. Normal adult individual exhibiting tendency toward loose coiling.

PLATE XXXI, fig. 9.—*Fulgur canaliculatum* Say. Recent. Atlantic City, N. J. Length = 170 mm. Normal adult individual.

Fig. 10.—*Fulgur canaliculatum* Say. Recent. Longport, N. J. Length = 168 mm. Adult individual which has been injured early in life and exhibits extra-specific adventitious senility.

Fig. 11.—*Fulgur pyrum* Dillw. Recent. Cards Sound, Dade County, Fla. Length = 81 mm. Normal adult individual. Introduced for comparison with fig. 10.

Fig. 12.—*Fulgur maximum* Con. Miocene. Yorktown, Va. Length = 165 mm. Adult individual exhibiting extreme senility—very heavy thick shell, irregular growth lines, discontinuous ornamentation and a large swelling on the anterior or branchial siphon.



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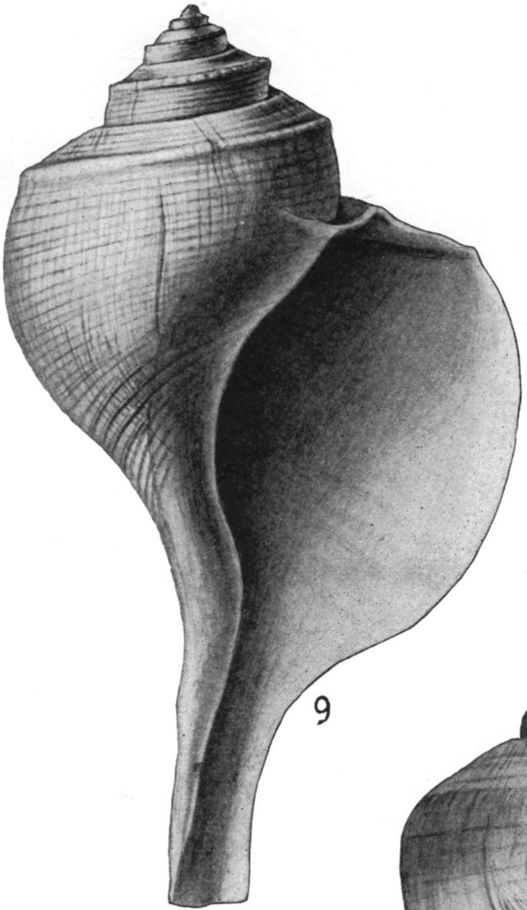

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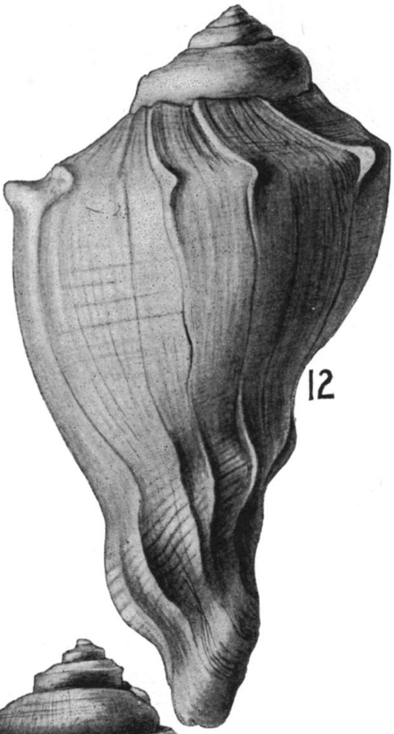

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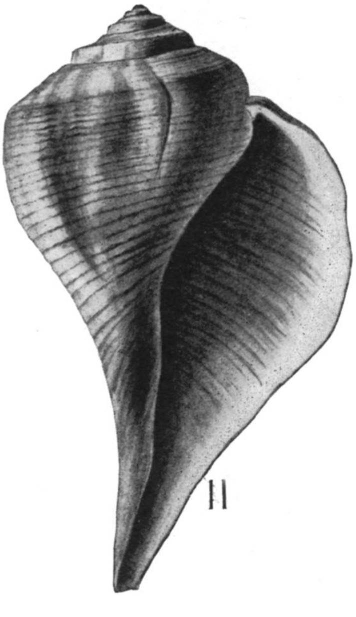

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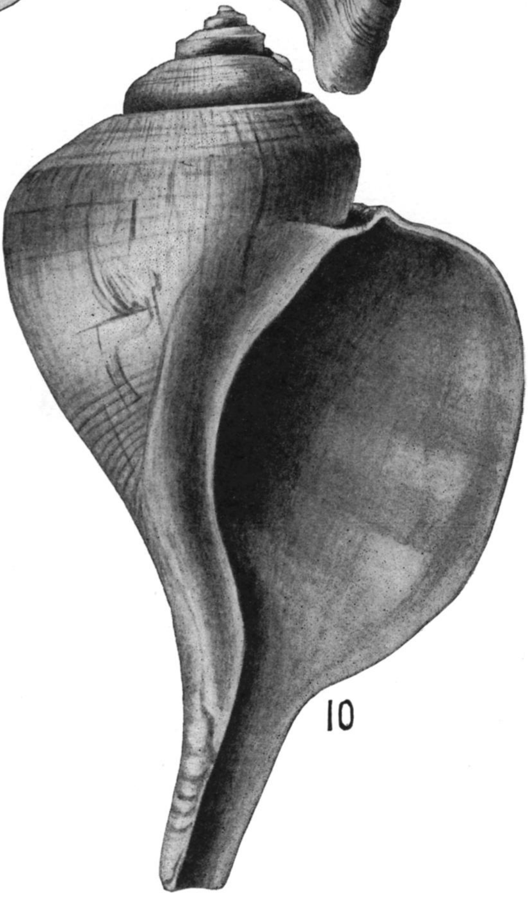

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